

Biology of Palaearctic *Wainia* bees of the subgenus *Caposmia* including a short review on snail shell nesting in osmiine bees (Hymenoptera, Megachilidae)

Andreas Müller¹, Christophe Praz², Achik Dorchin³

1 *ETH Zurich, Institute of Agricultural Sciences, Biocommunication and Entomology, Schmelzbergstrasse 9/LFO, 8092 Zurich, Switzerland* **2** *University of Neuchâtel, Institute of Biology, Evolutionary Entomology, Emile-Argand 11, 2000 Neuchâtel, Switzerland* **3** *School of Zoology, The Steinhardt Museum of Natural History, Tel Aviv University, 69978 Tel Aviv, Israel*

Corresponding author: Andreas Müller (andreas.mueller@usys.ethz.ch)

Academic editor: M. Ohl | Received 22 June 2018 | Accepted 10 August 2018 | Published 27 August 2018

<http://zoobank.org/ED9C1055-3472-487D-B725-EEAD6B92C721>

Citation: Müller A, Praz C, Dorchin A (2018) Biology of Palaearctic *Wainia* bees of the subgenus *Caposmia* including a short review on snail shell nesting in osmiine bees (Hymenoptera, Megachilidae). *Journal of Hymenoptera Research* 65: 61–89. <https://doi.org/10.3897/jhr.65.27704>

Abstract

Wainia, a species-poor genus of osmiine bees, contains two Palaearctic species, whose biologies are unknown. In the present publication, we describe the nesting site and nest architecture of *W. sexsignata* and analyse the pollen host spectra of *W. sexsignata* and *W. eremoplana* by microscopical analysis of larval faeces and female scopal contents. *W. sexsignata* nests in empty snail shells. It uses large petal pieces of yellow flowered Asteroideae to separate the linearly arranged brood cells and to construct a series of partitions between the outermost cell and the final nest closure, which consists of masticated green leaves. *W. sexsignata* is recorded as a new host of the meloid beetle *Sitarobrachys thoracica*. Both Palaearctic *Wainia* species have a strong preference for Asteraceae as pollen hosts, but occasionally also collect pollen on other plant taxa. A literature survey revealed that nesting in empty snail shells is widespread among osmiine bees: obligate snail shell nesting is assumed to have independently evolved at least twelve times in their evolutionary history and to occur in at least 56 species belonging to 4 genera and 14 subgenera.

Keywords

Apiformes, Asteroideae, Carduoideae, desert, DNA barcoding, host plant preference, nesting behaviour, *Sphincterochila*

Introduction

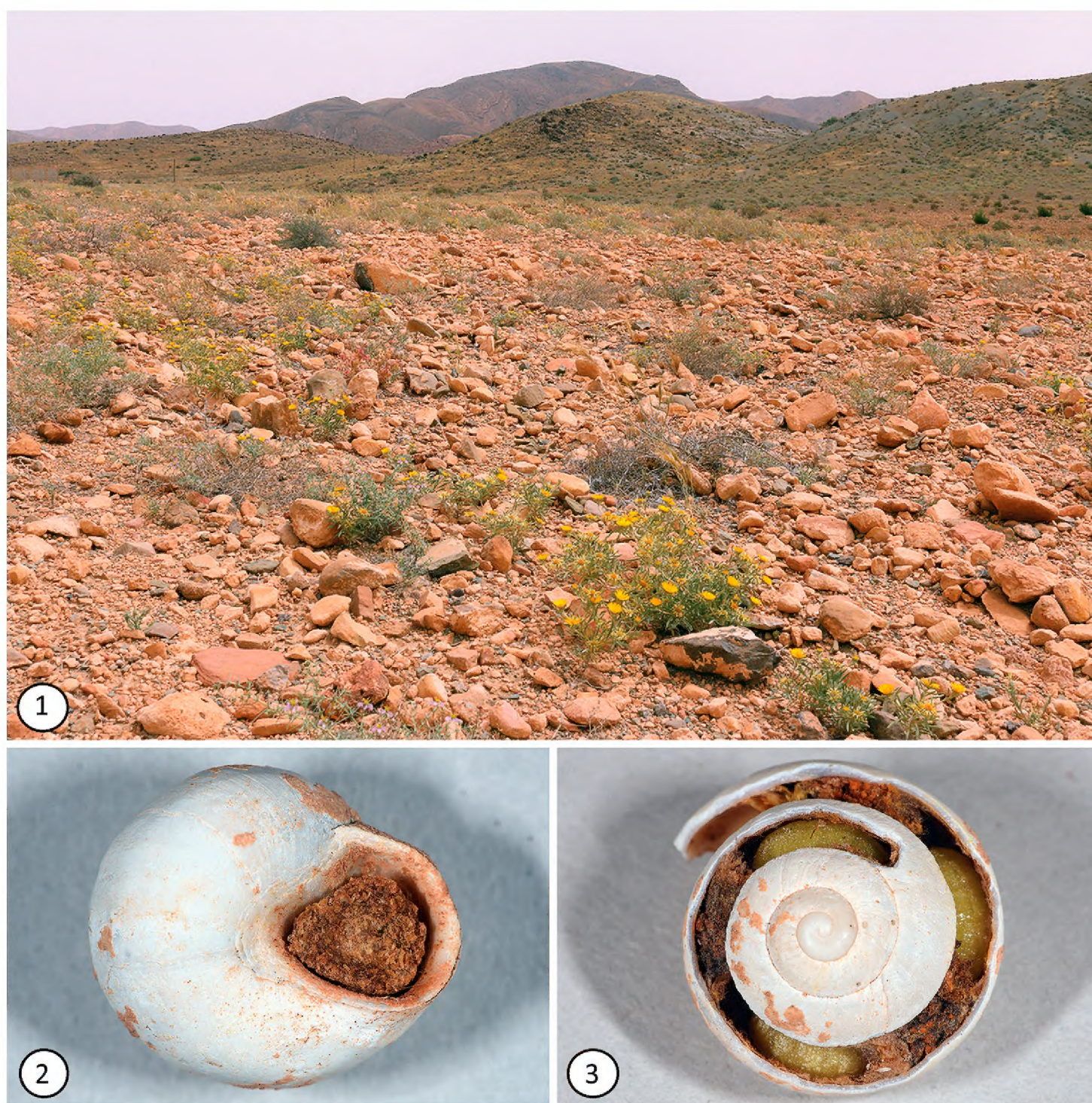
Wainia Tkalců is a species-poor genus of osmiine bees (Megachilidae, Osmiini) restricted to the eastern hemisphere and comprising 11 described species (Michener 2007, Müller 2018a). Within the Osmiini, it belongs to the *Osmia* group and is sister to a clade composed of the genera *Ashmeadiella* Cockerell, *Atoposmia* Cockerell and *Osmia* Panzer (Praz et al. 2008a, Rightmyer et al. 2013, Sedivy et al. 2013a; Fig. 13). *Wainia* is currently divided into three subgenera, with the subgenus *Caposmia* Peters being the most diverse with eight described species (Michener 2007, Kuhlmann et al. 2011, Müller 2018a). *Wainia* (*Caposmia*) has a disjunct distribution with six species occurring in the Afrotropics and two species distributed in the southern Palaearctic. The two Palaearctic species are *W. sexsignata* (Benoist) known only from southern Morocco and northern Western Sahara and *W. eremoplana* (Mavromoustakis) ranging from Tunisia over Egypt to the Levant. Both species are typical inhabitants of stony deserts and semideserts, where they often occur in dry riverbeds that provide the required floral resources during the bees' main flight period in March and April (Figs 1, 12).

The biology of the two Palaearctic *Wainia* species is unknown. In contrast, five Afrotropical species were found or strongly supposed to nest in empty snail shells (Peters 1984, Kuhlmann et al. 2011 and references therein, Müller 2018a), suggesting that snail shell nesting might be a widespread or even subgeneric trait of *Wainia* (*Caposmia*) including the Palaearctic species. During an excursion in spring 2017 to the Guelmim-Oued Noun region in southern Morocco, which lies within the known range of *W. sexsignata*, we collected numerous snail shells that contained finished bee nests as indicated by the presence of nest seals built from mud or chewed leaves. While the majority of these shells later turned out to be nests of *Hoplitis* (*Hoplitis*) *fertoni* (Pérez) and *Osmia* (*Hoplosmia*) *pinguis* Pérez, the nest architecture of two nests strongly resembled that described for southern African *Wainia* (*Caposmia*) species (Gess and Gess 1999, 2008, 2014, Kuhlmann et al. 2011). Unfortunately, no adults developed in these two nests rendering the assumption that they had been built by *W. sexsignata* hypothetical.

In the present contribution, we i) use DNA barcoding technique to prove that *Wainia sexsignata* did construct the putative *Wainia* nests from Morocco, ii) describe the nest of *W. sexsignata* and compare its architecture with that of the nests of Afrotropical *W.* (*Caposmia*) species, iii) analyse the pollen host preferences of both Palaearctic *W.* (*Caposmia*) species by microscopical pollen analysis of larval faeces and female scopal contents and iv) give a short review on snail shell nesting in osmiine bees.

Methods

Nests of snail shell nesting bees were collected 2.75 km southwest of Ifrane Atlas-Saghir (29°12.18'N, 09°30.32'W, 750m a.s.l.) in the province of Guelmim in southern Morocco on 17 April 2017. Ifrane Atlas-Saghir is characterized by an arid climate with



Figures 1–3. *Wainia sexsignata*. **1** Nesting habitat 2.75 km southwest of Ifrane Atlas-Saghir in southern Morocco (photo V. Mauss) **2** Nest in a shell of *Sphincterochila* spec. closed with a plug built from chewed leaves **3** Opened nest with three linearly arranged brood cells each containing a prepupa.

a mean annual temperature of 17.3 °C and a mean annual precipitation of 170 mm (<https://en.climate-data.org/location/715098>). The two presumed nests of *Wainia sexsignata* were found on a stony and sparsely vegetated plain adjacent to a dry riverbed (Fig. 1). The main plants flowering at the site were *Asteriscus graveolens* (Forssk.) Less. (Fig. 10) and *Cladanthus arabicus* (L.) Cass. (Asteraceae), *Convolvulus trabutianus* Schweinf. & Muschl. (Convolvulaceae) and species of *Kickxia* (Plantaginaceae), *Trichodesma* and *Echium* (Boraginaceae). The collected snail shell nests were opened in the lab in December 2017 to analyse their contents and the nest architecture. In the two presumed nests of *W. sexsignata*, which contained three brood cells each, five larvae had died within their cocoons after having reached the prepupal stage and one brood cell was occupied by the pupa of a blister beetle (Meloidae), which had infested the

cell (see Results). Bee prepupae and beetle pupa were stored in alcohol. To analyse the pollen content of the former larval provisions, faecal pellets from each of the six brood cells were dissolved in a drop of distilled water on a microscope slide and subsequently embedded in glycerol gelatine. Pollen grains contained in the larval faeces were identified with a light microscope at 400× magnification by comparing them with reference pollen slides of plant taxa that were flowering at the site where the *Wainia* nests had been found. Identification of the digested pollen was in most cases still possible since the structure of the pollen exine is not destroyed during the digestion process. The proportions of the different pollen types were estimated separately for each of the six brood cells to the nearest 10%.

DNA barcoding was performed with one dead prepupa originating from one of the two snail shell nests and a leg of a female of *Wainia sexsignata* collected on 18 April 2017 near Sidi Ifni (29°15.13'N, 10°16.93'W), about 75 km from the site where the presumed *Wainia* nests had been found. DNA was extracted with a “NucleoSpin Tissue” kit (Macherey-Nagel) following the manufacturer’s protocol. The 658 base-pair-long barcoding fragment of the mitochondrial gene Cytochrome Oxidase I was amplified using the primers LepF and LepR (Hebert et al. 2004). PCR products were purified enzymatically using a mix of the enzymes Exonuclease and FastAP Thermosensitive Alkaline Phosphatase (Fermentas). Sequencing was performed bidirectionally by an external company (Microsynth AG) using the primers used for the PCR. Chromatograms were edited and assembled in Geneious R6 (Kearse et al. 2012). Both consensus sequences were submitted to Genbank (Genbank accession numbers MH760429 and MH760430).

To uncover the pollen host preferences of *Wainia eremoplana*, the scopal pollen contents of 50 females collected at 21 different localities in Israel and Palestine (n = 47), Jordan (n = 2) and Tunisia (n = 1) were microscopically analyzed applying the method outlined by Westrich and Schmidt (1986). Before removing pollen from the metasomal scopae, the degree to which they were filled was estimated. The amount of pollen in the scopae was assigned to five classes, ranging from 5/5 (full load) to 1/5 (filled to one-fifth). The pollen grains were stripped off the scopae with a fine needle and embedded in glycerol gelatine on a slide. When a pollen load was composed of different pollen types, their percentages were estimated by counting the grains along two transects chosen randomly across the cover slip at a magnification of 400×. Pollen types represented by less than 5% of the counted grains were excluded to prevent a potential bias caused by contamination. For pollen loads consisting of two or more different pollen types, the percentages of the number of pollen grains were corrected by their volume. After assigning different weights to scopae according to their degree of filling (full loads were weighted five times more strongly than scopae filled to only one-fifth), the estimated percentages were summed up over all pollen samples. The pollen grains were identified at a magnification of 400× with the aid of the literature cited in Westrich and Schmidt (1986), Beug (2004) and an extensive reference collection.

The description of the pollen collecting behaviour of *Wainia eremoplana* is based on field observations made in Jordan in the Wadi al Hasa south of Al-Karak (30°57.51'N, 35°45.50'E) on 20 April 2007.

Results

DNA barcoding

The chromatograms obtained from both prepupa and adult of *Wainia sexsignata* were clean. Translations to amino acids revealed that none of the sequences contained stop codons. Blast searches on Genbank and identification requests on BOLD indicated that neither sequence appeared to be close (>90% similarity) to any previously published sequence. The closest matches (approximately 88% similarity) were to diverse osmiine bee taxa (no sequence of *Wainia* (*Caposmia*) is available for this mitochondrial fragment). Both sequences were nearly identical to each other and differed by a single nucleotide on position 214, corresponding to an uncorrected genetic distance of 0.18%. This single point mutation is in a third codon position and is silent. Consequently, even if both sequences are not 100% identical it can confidently be concluded that the analyzed prepupa belongs to *W. sexsignata*.

Architecture of the nest of *Wainia sexsignata*

The two nests of *W. sexsignata* were already closed when they were discovered. Each nest was built in an empty snail shell of *Sphincterochila* sp. (Sphincterochilidae) with a maximal diameter of 19 mm (Figs 2, 3). The two nests were not hidden among vegetation or under stones but lay openly on the stony and sparsely vegetated ground in a distance of few meters from each other. No traces of leaf pulp were visible on the outside of the shells, indicating that the female bees did not glue patches of leaf pulp onto the shell surface as many other snail shell nesting osmiine bees do (see Discussion). The two nests were not sealed against their rear end with a basal wall. Both had a very similar architecture except for minor differences in the construction of the nest plug and consisted of three brood cells each delimited towards the nest entrance by a cell partition (Fig. 3) and the nest plug that occupied the space between the outermost cell partition and the shell opening (Fig. 6).

The brood cells were arranged in a linear series and had a length of 15–17 mm (Fig. 3). Each cell contained a dead prepupa spun in a dark brown cocoon of 11–13 mm length except for one cell that harboured a meloid beetle pupa (see below). The space between the front end of the cocoon and the cell partition was densely packed with faecal pellets over a distance of 3–5 mm. The cell partitions were very thin and consisted of two to four pieces of yellow petals, which either slightly overlapped or formed two petal layers tightly contacting each other. Two non- or only slightly overlapping petal pieces were sufficient to close the shell whorl. The petal pieces were arranged parallel to each other and almost perpendicular to the shell columella (Fig. 4). Small portions of leaf pulp were used to glue the petal pieces on either end to the lateral sides of the inner shell surface (Figs 4, 9). The petal pieces contacting the ceiling or the floor of the shell whorl were additionally fixed with leaf pulp to the shell surface along their lateral margins. However, the petal pieces



Figures 4–9. *Wainia sexsignata*. **4** Brood cell partition built from yellow petal pieces of Asteroidae, which are partly covered with dark brown remnants of the larval cocoon; note the portion of leaf pulp at the right upper side of the partition used to glue the petal pieces to the inner shell surface **5** Partition of the nest plug **6** Nest plug consisting of a series of four partitions constructed from yellow Asteroidae petal pieces immediately followed by the nest closure at the shell opening, which consists of leaf pulp; the partition at the extreme right is the outermost brood cell partition **7** Yellow petal pieces adhering to the rear side of the nest closure **8** Anterior part of the nest plug with an additional wall of leaf pulp built in front of the second outermost plug partition **9** Asteroidae petal pieces used to construct cell and plug partitions; petals in the upper row with traces of leaf pulp, which glued them to the inner shell surface.

were never agglutinated medially with leaf pulp among each other. Petal pieces used to construct the cell partitions were invariably yellow ligules of Asteroidae ray florets, which were usually bitten off close to their base (Fig. 9). In contrast, leaf pulp used to glue the petal pieces to the inner shell surface was collected on green leaves as could be judged from its greenish to brownish colour and the presence of star-shaped hairs in the pulp matrix.

The nest plug, which occupied the space between the outermost cell partition and the shell opening, had a length of 9 mm and 11 mm, respectively. It consisted of four and six partitions, respectively (Fig. 6), which were evenly distributed over a distance of 6 mm and 8 mm, respectively, and the 2–3 mm thick nest closure at the shell opening (Figs 6, 8). The plug partitions were constructed in exactly the same way and from exactly the same material as the cell partitions (Fig. 5) with the exception that they were slightly thicker consisting of five to six yellow petal pieces arranged in three layers immediately behind each other. The nest closure consisted of rather roughly masticated greenish and reddish leaf pulp without the addition of sand grains (Figs 2, 6, 8). While the former was collected on green leaves of unknown origin, the latter was probably harvested on the reddish perigons of a *Rumex* (Polygonaceae) species growing at the study site. The nest closure was built immediately adjacent to the outermost plug partition with the petal pieces of the latter tightly adhering to its rear side (Figs 7, 8). In the nest containing six plug partitions, an additional and slightly less than 1 mm thick wall of greenish leaf pulp was built in front of the second outermost partition (Fig. 8); again, the yellow petals of the plug partition adhered to the rear side of this wall.

The innermost brood cell of one nest harboured a pupa of the blister beetle *Sitarobrachys thoracica* (Kraatz) (Meloidae) encapsulated in the cast skins of its last larval instars. This species parasitizes brood cells of andrenid and megachilid bees (Bologna and Pinto 2002). It was found to develop in soil nests of *Andrena* spec. and *Hoplitis* (*Anthocopa*) *longispina* (Pérez), in mud nests of *Megachile* (*Chalicodoma*) *sicula* (Rossi) and in snail shell nests of *Hoplitis* (*Hoplitis*) *pallicornis* (Fries) (Stahlberg 1909, Andres 1910, Martínez de la Escalera 1914, Cros 1924, Kaszab 1957, Fauchaux 2011). *Wainia sexsignata* is a new host of this blister beetle species.

Pollen host preferences of *Wainia sexsignata* and *W. eremoplana*

The microscopical analysis of digested pollen grains in the larval faeces of *Wainia sexsignata* revealed that pollen of the Asteroideae (Asteraceae) was the near exclusive constituent of the former pollen provisions (Tab. 1). 96.6% of all pollen grains belonged to this subfamily, while 1.7% was assigned to the Scrophulariaceae and the remaining 1.7% could not be identified. The Asteroideae pollen in the larval faeces was exclusively of the *Aster* type. This suggests that *Asteriscus graveolens*, which richly flowered at the site where the *Wainia* nests were discovered (Fig. 10), was the main pollen host, which is in line with the observation of a female of *W. sexsignata* near Sidi Ifni visiting *A. graveolens* (see Methods). *Cladanthus arabicus* - the only other representative of the Asteroideae flowering at the study site - can be excluded as a pollen source since it possesses pollen grains of the *Anthemis* type.

Wainia eremoplana is mesolectic on Asteraceae and Brassicaceae (Tab. 2). Among the Asteraceae, the subfamily Asteroideae is by far the most important pollen source. Species of the Carduoideae are also frequently exploited (Fig. 11), whereas representatives of the Cichorioideae appear to be only very rarely used. Based on field data and label

Table 1. Pollen composition of larval faeces of *Wainia sexsignata* in two nests with three brood cells each.

		Asteraceae, Asteroideae	Scrophulariaceae	Unknown
nest 1	brood cell 1	100%		
	brood cell 2	100%		
	brood cell 3	100%		
nest 2	brood cell 1	90%	10%	
	brood cell 2	100%		
	brood cell 3	90%		10%

Table 2. Pollen composition of female pollen loads of *Wainia eremoplana*. n = 50 pollen loads from 21 different localities in Israel and Palestine (n = 47), Jordan (n = 2) and Tunisia (n = 1).

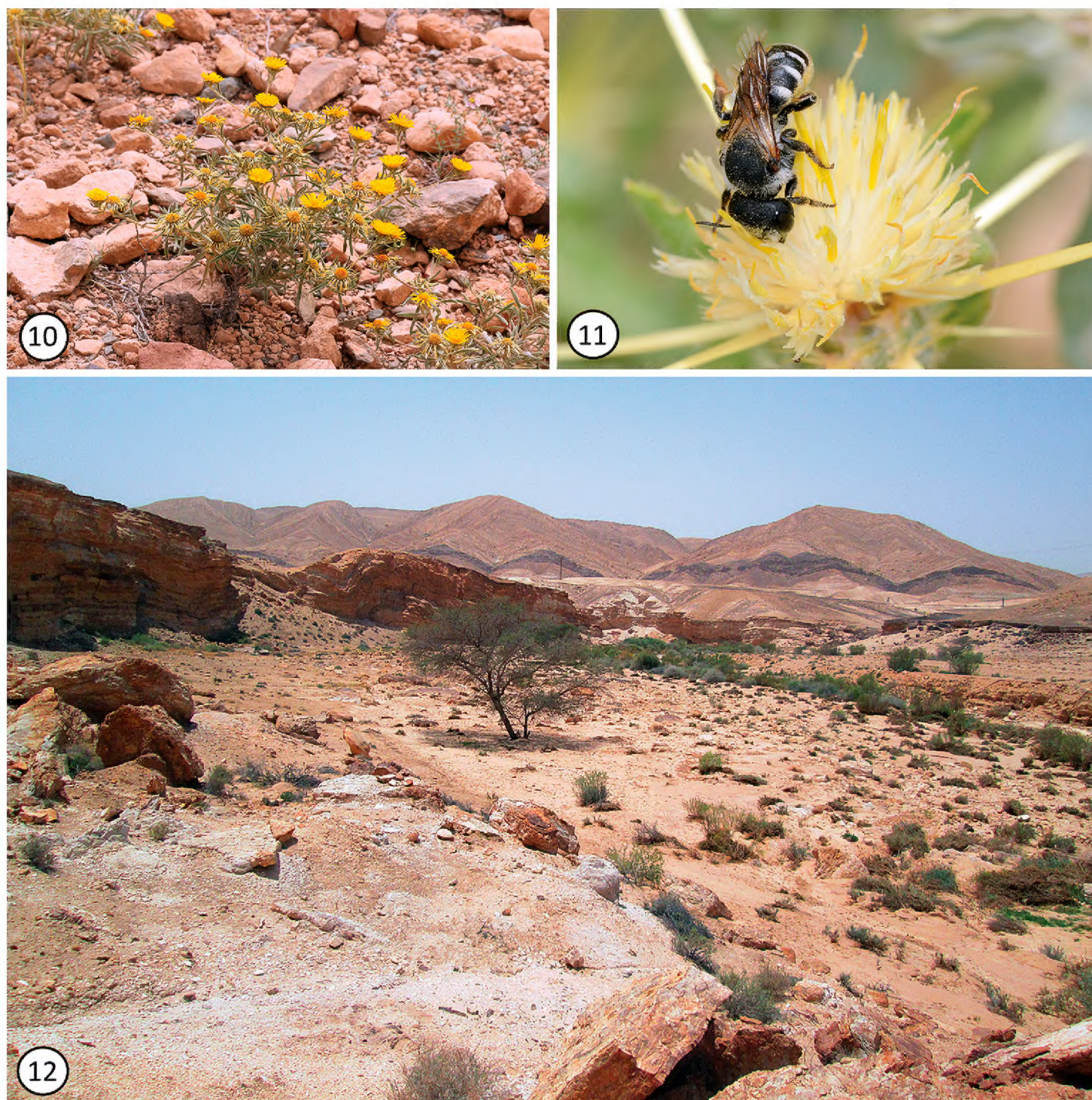
Plant family	Plant subfamily	% pollen grain volume	number of loads with this pollen type	number of pure loads
Asteraceae		92.0	50 (100%)	23 (46%)
Asteraceae	Asteroideae	78.9	47 (94%)	14 (28%)
Asteraceae	Carduoideae	12.4	13 (26%)	2 (4%)
Asteraceae	Cichorioideae	0.7	1 (2%)	0 (0%)
Brassicaceae		8.0	27 (54%)	0 (0%)

records, *Anthemis* spec., *Chrysanthemum coronarium*, *Pulicaria incisa* and *Senecio* spec. serve as pollen hosts among the Asteroideae and *Centaurea hyalolepis* and thistles among the Carduoideae. Pollen uptake from the Asteraceae flower heads involves rapid up and down movements of the metasoma against the pollen-bearing florets. On the Asteroideae, pollen is taken up directly into the metasomal scopa without the aid of the hind legs, whereas on Carduoideae the hind legs are involved in directing the florets under the seesawing metasoma. Pollen of Brassicaceae was recorded in 27 out of the 50 pollen loads analysed (Tab. 2). However, none of the loads was composed of Brassicaceae pollen alone, only one load contained more than 50% Brassicaceae pollen and the proportion of Brassicaceae pollen was overall rather low with an average of 19% per load. Nectar is occasionally also taken from other plant taxa than Asteraceae and Brassicaceae. Based on label records, several specimens of *W. eremoplana* were collected on *Commicarpus hazeva* in Israel, suggesting that this Nyctaginaceae species has served as a nectar source.

Discussion

Architecture of the nests of *Wainia*

The use of large petal pieces to construct both cell and plug partitions and the presence of a series of partitions evenly distributed in the space between the outermost cell partition and the nest closure as observed in *Wainia sexsignata* are unique characteristics among the Palaearctic osmiine bees. Both characteristics, however, were also recorded in



Figures 10–12. **10** *Asteriscus graveolens* (Asteroideae, Asteraceae), an important pollen host of *Wainia sexsignata* (photo V. Mauss) **11** Female of *Wainia eremoplana* collecting pollen on *Centaurea* spec. (photo G. Pisanty) **12** Habitat of *Wainia eremoplana* in the central Negev Desert of Israel at Nahal Hatira (the large crater), 10 km east of Yeroham.

two snail shell nesting Afrotropical *W.* (*Caposmia*) species (Gess and Gess 1999, 2008, 2014, Kuhlmann et al. 2011). In *W. atrorufa* (Friese) and *W. gessorum* Kuhlmann, the thin partitions between the brood cells also consist of large pieces of petals arranged at right angles to the shell columella (Gess and Gess 2014), and the space in front of the outermost brood cell is filled with a succession of partitions constructed from petal pieces (Gess and Gess 1999, but see Gess and Gess 2008, 2014 for a slightly deviating description). In contrast to *W. sexsignata*, however, the nest closure at the shell opening does not consist solely of leaf pulp but rather is a combination of “cemented sand and plant matter” (Gess and Gess 1999). The petals used by the two Afrotropical species for nest construction possibly originated from *Griehum* (Neuradaceae) (S. Gess personal

communication). However, as *Griekum* species have yellow flowers like several Asteraceae species growing in the same habitat, it cannot be excluded that the bees actually harvested yellow Asteraceae flowers for nest construction as in the Palearctic *W. sexsignata* (see discussion on possible pollen hosts of *W. atrorufa* below). In summary, apart from slight differences in the material used for the outermost nest closure and possibly differing petal sources, the nesting biologies of the two Afrotropical *W. (Caposmia)* species and the Palearctic *W. sexsignata* are identical, suggesting close relatedness.

In contrast, the snail shell nests of the Afrotropical *Wainia (Caposmia) elizabethae* (Friese) substantially differ from those of the three *W. (Caposmia)* species addressed above (Gess and Gess 2008, 2014, Kuhlmann et al. 2011). In *W. elizabethae*, the brood cell partitions and the single-walled nest closure consist of sand grains, which are cemented together with an unidentified resinous substance (which might possibly be saliva; S. Gess personal communication), and the space between the outermost brood cell and the nest closure is loosely filled with sand. The differing nest building material and deviating nest architecture of *W. elizabethae* indicate a considerable variability in the nesting biology of *W. (Caposmia)* species, which is unusual for osmiine bee subgenera, where nest architecture and nest building material are often highly conserved (Müller 2018a).

Beside the four species discussed above, the South African *Wainia (Caposmia) braunsi* (Peters) was reared from snail shells (Peters 1984). A further Afrotropical species, *W. (Caposmia) algoensis* (Brauns), is probably also a snail shell nester (Kuhlmann et al. 2011, Gess and Gess 2014). Therefore, the selection of empty snail shells as a nesting site appears to be a subgeneric trait of *Wainia (Caposmia)*.

Pollen host preferences of *Wainia*

Pollen analysis of larval faeces of *Wainia sexsignata* and female scopal contents of *W. eremoplana* revealed a strong affiliation of both species to the Asteraceae, particularly to the Asteroideae and to a lesser extent also to the Carduoideae. However, neither species is strictly oligolectic on Asteraceae. *W. eremoplana* regularly collects pollen also on Brassicaceae and pollen of Scrophulariaceae was recorded in the larval faeces of *W. sexsignata*. The finding that the larval faeces from four out of the six brood cells were exclusively composed of Asteroideae pollen indicates that the larvae of *W. sexsignata* are capable of developing on a pure Asteraceae pollen diet, thus being physiologically adapted to cope with the unfavourable properties of Asteraceae pollen, which has repeatedly been shown to hamper larval development of bee species not specialized on this plant family (Müller and Kuhlmann 2008, Praz et al. 2008b, Sedivy et al. 2011, Vanderplanck et al. 2018).

The pollen host preferences of the southern African *Wainia (Caposmia)* species have not been studied. Except for the observation of a single female of *W. atrorufa* visiting flowers of *Hermannia* (Malvaceae), no flower records exist (Kuhlmann et al. 2011, Gess and Gess 2014). However, the larval provisions in the brood cells of five nests

of *W. atrorufa* from two different localities were deep yellow and consisted of heavily sculptured and spiny pollen grains of 25 to 40 μm diameter (Gess and Gess 1999). These pollen characteristics clearly point to the Asteroideae, suggesting that *W. atrorufa* and possibly also other Afrotropical *W.* (*Caposmia*) species might exhibit a preference for Asteraceae pollen as the two Palaearctic species do.

Snail shell nesting in osmiine bees

Empty snail shells offer nesting opportunities for bees that build their brood cells within preexisting cavities. They appear to be well suited for nest construction for several reasons: i) the narrow and linear, albeit curved form of the shell cavity allows for the arrangement of the cells in a linear series and easy closure of the nest at the shell aperture; ii) the progeny are well protected by the considerable hardness of the shell and the usually white shell colour, which reflects the sunlight and thus might reduce the risk of overheating; iii) xeric habitats often harbour large numbers of empty snail shells providing numerous nesting opportunities; iv) the number of colonizable snail shells does not diminish over time due to the permanent renewal of the supply of dead shells; and v) the presence of empty snail shells enables colonization of habitats, e.g. (semi)arid areas, which naturally lack preexisting linear cavities such as insect burrows in dead wood or hollow plant stems used by innumerable bee species as nesting sites. On the other hand, nesting in exposed and movable snail shells may also entail disadvantages compared to nesting in the ground, in stems, in dead wood or in rock crevices: i) the larvae may have a higher risk of experiencing lethal temperatures by direct sunlight, particularly when they are still young and do not yet have reached the diapausing stage (see Müller et al. 2017); ii) nests, larval provisions or progeny may be more prone to parasitization or to predation, e.g. by small mammals or birds; and iii) flood events e.g. in dry riverbeds, which are important nesting habitats of bees in (semi)deserts, may destroy a larger proportion of the nests by sweeping them away.

Records of snail shell nesting species exist for all three main bee taxa that occupy preexisting cavities as nesting sites, i.e. Megachilini, Anthidiini and Osmiini (Megachilidae). However, the proportion of snail shell nesters substantially differs among these three taxa. Snail shell nesting in the Megachilini appears to be almost absent. The only record of a snail shell nesting megachiline bee refers to the Palaearctic *Megachile* (*Chalicodoma*) *lefebvrei* (Lepeletier), which usually constructs its brood cells in holes of stones and rocks (Ferton 1908), but facultatively also colonizes snail shells (Ferton 1920). Among the Anthidiini, snail shell nesting has been observed only in four Palaearctic species of the genus *Rhodanthidium* (Pasteels 1977 and references therein, Erbar and Leins 2017) and in two Afrotropical species of the genus *Afranthidium* (Gess and Gess 1999, 2008, 2014), most of which seem to be obligate snail shell nesters. The great majority of bees colonizing snail shells belongs to the Osmiini. Snail shell nesting has been recorded in 52 osmiine bee species belonging to 5 genera and 14 subgenera (Tab. 3). Among these species, representatives of the genus *Osmia* predominate with 35 spe-

Table 3. Osmiine bee species recorded to nest in empty snail shells. Nea = Nearctic, Afr = Afrotropics, Pal = Palearctic; obl = obligatory nesting in snail shells; fac = facultatively nesting in snail shells.

Species	Biogeographic region	User type	Alternative nesting sites	References
<i>Ashmeadiella</i> (<i>Ashmeadiella</i>) spec.	Nea	?	?	Michener (1939), Hurd and Michener (1955)
<i>Hoplitis</i> (<i>Anthocopa</i>) <i>conchophila</i> Kuhlmann	Afr	obl	—	Gess and Gess (1999, 2008, 2014), Kuhlmann et al. (2011)
<i>Hoplitis</i> (<i>Hoplitis</i>) <i>fertoni</i> (Pérez)	Pal	obl	—	Ferton (1890, 1908), Le Goff (2003), Sedivy et al. (2013b)
<i>Hoplitis</i> (<i>Hoplitis</i>) <i>pallicornis</i> (Friese)	Pal	fac	holes in stones	Stahlberg (1909), Gogala (1999)
<i>Hoplitis</i> (<i>Tkalcula</i>) <i>zandeni</i> (Teunissen and van Achterberg)	Pal	obl	—	Müller and Mauss (2016)
<i>Hoplitis</i> (<i>Tkalcula</i>) spec. nov.	Pal	obl	—	A. Müller (unpublished data)
<i>Osmia</i> (<i>Allosmia</i>) <i>bischoffi</i> Atanassov	Pal	obl	—	Atanassov (1938), A.W. Ebmer (personal communication)
<i>Osmia</i> (<i>Allosmia</i>) <i>lhotelleriei</i> Pérez	Pal	obl	—	Ferton (1890, as <i>O. fossoria</i>), O'Toole and Raw (1991)
<i>Osmia</i> (<i>Allosmia</i>) <i>melanura</i> Morawitz	Pal	obl	—	Müller (1992)
<i>Osmia</i> (<i>Allosmia</i>) <i>rufohirta</i> Latreille	Pal	obl	—	Bellmann (1981), Bonelli (1972), Ferton (1894, 1897), Grandi (1961), Grozdanic (1969), Westrich (1989)
<i>Osmia</i> (<i>Allosmia</i>) <i>rutila</i> Erichson	Pal	obl	—	Haeseler (1997)
<i>Osmia</i> (<i>Allosmia</i>) <i>sybarita</i> Smith	Pal	obl	—	Mavromoustakis (1939, 1948a), O'Toole and Raw (1991), Haeseler (1997), Vereecken and Le Goff (2012)
<i>Osmia</i> (<i>Diceratosmia</i>) <i>conjuncta</i> Cresson	Nea	obl?	—	Rau (1937)
<i>Osmia</i> (<i>Diceratosmia</i>) <i>marilaunidii</i> Cockerell	Nea	?	?	Cane et al. (2007, as <i>O. botitena</i>), Griswold and Rightmyer (2017)
<i>Osmia</i> (<i>Diceratosmia</i>) <i>subfasciata</i> Cresson	Nea	fac	insect burrows in dead wood; wooden trap nest blocks; hollow stems; abandoned cells of <i>Sceliphron</i>	Linsley (1946), Hurd and Michener (1955), Mitchell (1962), Krombein (1967), Neff and Simpson (1992)
<i>Osmia</i> (<i>Erythrosmia</i>) <i>andrenoides</i> Spinola	Pal	obl	—	Ferton (1894, 1908), Benoist (1931), Ducke (1900), Stoeckert (1933), Westrich (1989), A. Müller (unpublished data)
<i>Osmia</i> (<i>Helicosmia</i>) <i>aurulenta</i> (Panzer)	Pal	obl	—	Alfken (1914), Friese (1923), Maréchal (1926), Bonelli (1971), Bellmann (1981), Westrich (1989)
<i>Osmia</i> (<i>Helicosmia</i>) <i>clypearis acuta</i> Warncke	Pal	?	?	A. Müller, C. Praz and C. Sedivy (unpublished data)

Species	Biogeographic region	User type	Alternative nesting sites	References
<i>Osmia (Helicosmia) melanogaster</i> Spinola	Pal	fac	insect burrows in dead wood, hollow stems	Ferton (1892), Banaszak and Romasenko (2001)
<i>Osmia (Helicosmia) notata</i> (Fabricius)	Pal	fac	cavities in stones, insect burrows in the ground	Ferton (1914, as <i>O. decemsignata</i>), C. Sedivy, C. Praz and A. Müller (unpublished data)
<i>Osmia (Helicosmia) orientalis</i> Benoist	Pal	obl	—	Maeta (1978), Kandori et al. (2010)
<i>Osmia (Hoplosmia) carbo</i> (Zanden)	Pal	obl	—	Mavromoustakis (1948b, as <i>O. pinguis</i>), Müller (2018b)
<i>Osmia (Hoplosmia) croatica</i> Friese	Pal	obl	—	Müller (2018b)
<i>Osmia (Hoplosmia) fallax</i> Pérez	Pal	obl	—	Moreno-Rueda et al. (2008), J. Ortiz-Sanchez (personal communication)
<i>Osmia (Hoplosmia) pinguis</i> Pérez	Pal	obl	—	Ferton (1920), Müller (2018b)
<i>Osmia (Hoplosmia) spinigera</i> Latreille	Pal	obl	—	Müller (2018b)
<i>Osmia (Hoplosmia) spinulosa</i> (Kirby)	Pal	obl	—	Friese (1893), Gehrs (1902), Stoeckhert (1933), Grandi (1961), Romasenko (1980), Müller (1994, 2018b)
<i>Osmia (Neosmia) bicolor</i> (Schrank)	Pal	obl	—	Friese (1897, 1923), Grozdanic and Vasic (1965), Amiet (1973), Bellmann (1981), Westrich (1989)
<i>Osmia (Neosmia) cinnabarina</i> Pérez	Pal	obl	—	A. Müller (unpublished data)
<i>Osmia (Neosmia) jason</i> Benoist	Pal	obl	—	Grozdanic (1971, as <i>O. aff. gracilicornis</i>)
<i>Osmia (Neosmia) rufigastra</i> Lepeletier	Pal	obl	—	Ferton (1920)
<i>Osmia (Neosmia) scutispina</i> Gribodo	Pal	obl	—	C. Sedivy, C. Praz and A. Müller (unpublished data)
<i>Osmia (Neosmia) tingitana</i> Benoist	Pal	obl	—	Peters (1977), Sihem et al. (2017)
<i>Osmia (Osmia) bicornis</i> (Linnaeus)	Pal	fac	wide spectrum of cavities of diverse form and size	Friese (1923), Raw (1972), Westrich (1989 and references therein), Vicens et al. (1993)
<i>Osmia (Osmia) cornuta</i> (Latreille)	Pal	fac	wide spectrum of cavities of diverse form and size	Friese (1923), Westrich (1989 and references therein), Vicens et al. (1993), G. Le Goff (personal communication)
<i>Osmia (Osmia) tricornis</i> Latreille	Pal	fac	insect burrows in dead wood; hollow stems; insect burrows in the ground	Benoist (1931), Vicens et al. (1993, 1994), A. Müller (unpublished data)
<i>Osmia (Pyrosmia) ferruginea</i> Latreille	Pal	fac	hollow stems	Ferton (1890, 1897), Saunders (1908), Alfken (1914), Benoist (1931), Mavromoustakis (1939, 1952), Grandi (1961), Haeseler (1997), Moreno-Rueda et al. (2008)
<i>Osmia (Pyrosmia) gemmea</i> Pérez	Pal	obl?	—	Morice (1900), Alfken (1942, as <i>O. ligulicornis</i>), Zanden (1991)

Species	Biogeographic region	User type	Alternative nesting sites	References
<i>Osmia</i> (<i>Pyrosmia</i>) <i>lobata</i> Friese	Pal	?	?	Ferton (1914, as <i>O. leucopgya</i>)
<i>Osmia</i> (<i>Pyrosmia</i>) <i>versicolor</i> Latreille	Pal	obl	—	Benoist (1931), Ferton (1890, 1901), Moreno-Rueda et al. (2008), Westrich (1989)
<i>Osmia</i> (<i>Pyrosmia</i>) <i>viridana</i> Morawitz	Pal	fac	holes in rocks; abandoned cells of <i>Megachile</i> (<i>Chalicodoma</i>)	Ferton (1901), Benoist (1931), Mavromoustakis (1939, 1948a, 1957), Amiet et al. (2004)
<i>Protosmia</i> (<i>Protosmia</i>) <i>exenterata</i> (Pérez)	Pal	obl?	—	Ferton (1894)
<i>Protosmia</i> (<i>Protosmia</i>) <i>glutinosa</i> (Giraud)	Pal	fac	abandoned cells of <i>Anthophora</i> , <i>Megachile</i> (<i>Chalicodoma</i>) and <i>Sceliphron</i> ; cavities in the ground; insect burrows in the ground	Giraud (1871), Popov (1961), Moreno-Rueda et al. (2008), J. Ortiz-Sanchez (personal communication)
<i>Protosmia</i> (<i>Protosmia</i>) <i>paradoxa</i> (Friese)	Pal	obl?	—	Mavromoustakis (1939)
<i>Protosmia</i> (<i>Protosmia</i>) <i>sideritis</i> Tkalcù	Pal	obl?	—	Tkalcù (1978)
<i>Protosmia</i> (<i>Protosmia</i>) <i>stelidoides</i> (Pérez)	Pal	obl?	—	Ferton (1894, 1908)
<i>Protosmia</i> (<i>Protosmia</i>) <i>tauricola</i> Popov	Pal	obl?	—	Banaszak and Romasenko (2001)
<i>Wainia</i> (<i>Caposmia</i>) <i>atrorufa</i> (Friese)	Afr	obl	—	Gess and Gess (1999, 2008, 2014), Kuhlmann et al. (2011)
<i>Wainia</i> (<i>Caposmia</i>) <i>braunsi</i> (Peters)	Afr	obl?	—	Peters (1984)
<i>Wainia</i> (<i>Caposmia</i>) <i>elizabethae</i> (Friese)	Afr	obl	—	Gess and Gess (1999, 2008, 2014), Kuhlmann et al. (2011)
<i>Wainia</i> (<i>Caposmia</i>) <i>gessorum</i> Kuhlmann	Afr	obl	—	Gess and Gess (1999, 2008, 2014), Kuhlmann et al. (2011)
<i>Wainia</i> (<i>Caposmia</i>) <i>sexsignata</i> (Benoist)	Pal	obl	—	this study

cies that exclusively or facultatively nest in snail shells. Snail shell nesting is much more common in Palaearctic osmiine bees (4 genera/11 subgenera/43 species) than in the Osmini from the Afrotropics (2/2/5) and the Nearctic (2/2/4). The low proportion of snail shell nesters in the Afrotropics may be explained by the distinctly lower diversity of osmiine bees south of the Sahara compared to both the Palaearctic and the Nearctic fauna (Ascher and Pickering 2018). However, the almost complete absence of snail shell nesters in the Nearctic, which encompasses about 30% of the worldwide osmiine bee diversity in terms of described species (Ascher and Pickering 2018), remains enigmatic and can neither be explained by an overall scarceness of snails in North America nor by a poorer knowledge of Nearctic osmiine bee biology.

The snail shell nesting osmiine bees can be divided into two groups (Tab. 3). The representatives of the first group nest in various preexisting cavities and occasionally also colonize snail shells. Some species of these facultative snail shell nesters, such as *Osmia* (*Osmia*) *bicornis*, *O.* (*Osmia*) *cornuta*, *O.* (*Osmia*) *tricornis* or *O.* (*Helicosmia*) *notata*, only exceptionally utilize snail shells. If they do, they usually colonize large shells and often place their brood cells side by side rather than in a linear series (Tab. 4, Fig. 14), conforming to their ability to use cavities of widely different shapes and sizes for nesting. Other species of this first group, such as *Osmia* (*Pyrosmia*) *ferruginea* or *O.* (*Pyrosmia*) *viridana* (Fig. 20) frequently nest in snail shells but are not entirely dependent on them and occasionally also colonize other preexisting cavities. The representatives of the second group exclusively nest in empty snail shells and appear to have lost the flexibility to colonize alternative nesting sites. For these species, no nesting sites other than snail shells have ever been reported and they often belong to clades entirely composed of snail shell nesters. Though the assignment to one of these two groups is tentative for several species due to the low number of nests reported so far (Tab. 3), at least 56 osmiine bee species belonging to 4 genera and 14 subgenera are assumed to be obligate snail shell nesters, which corresponds to about 5% of the described osmiine bee species diversity (Ascher and Pickering 2018, Müller 2018a). Included in these figures are all species of *Hoplitis* (*Tkalcua*), *Osmia* (*Allosmia*), *O.* (*Erythrosmia*), the *O. spinulosa* species group of *O.* (*Hoplosmia*), *O.* (*Neosmia*) and *Wainia* (*Caposmia*), irrespective of whether they have been recorded to nest in snail shells or not. In these taxa, snail shell nesting is most probably a subgeneric or species group trait as all their representatives, for which information on the nesting biology is available, utilize snail shells as exclusive nesting sites. The percentage of obligate snail shell nesters is certainly higher than currently known. Several speciose taxa, such as *Hoplitis* (*Hoplitis*), *Osmia* (*Helicosmia*), *O.* (*Pyrosmia*) or *Protosmia* (*Protosmia*) are expected to contain additional species that exclusively nest in snail shells. Furthermore, species of other taxa, for which the nesting sites are still unknown, e.g. *Osmia* (*Nasutosmia*) or *Wainia* (*Wainiella*), might possibly turn out to be also snail shell nesters.

Based on available molecular phylogenies (Praz et al. 2008a, Rightmyer et al. 2013, Sedivy et al. 2013a), obligate snail shell nesting has likely evolved independently at least twelve times in the evolutionary history of the osmiine bees (Fig. 13): i) at least once in *Protosmia* (*Protosmia*), ii) once in *Hoplitis* (*Anthocopa*), iii) once in *Hoplitis* (*Hoplitis*), iv) once in the ancestor of *Hoplitis* (*Tkalcua*), v) once in the ancestor of *Wainia* (*Caposmia*), vi) once in the ancestor of the clade composed of *Osmia* (*Allosmia*) and *Osmia* (*Neosmia*) (but see below), vii) once in the ancestor of the *Osmia* (*Hoplosmia*) *spinulosa* species group (but see below), viii) once in the ancestor of *Osmia* (*Erythrosmia*), ix) at least once in *Osmia* (*Pyrosmia*), x) at least once in *Osmia* (*Diceratosmia*) and probably at least twice in *Osmia* (*Helicosmia*), i.e. in xi) *O. aurulenta* and xii) *O. orientalis*, which substantially differ in both adult morphology and nest architecture suggesting only distant relatedness.

Among the snail shell nesting osmiine bees, *Osmia* (*Allosmia*) and *O.* (*Neosmia*) are the only subgenera containing species that seal their nests with a mixture of leaf pulp

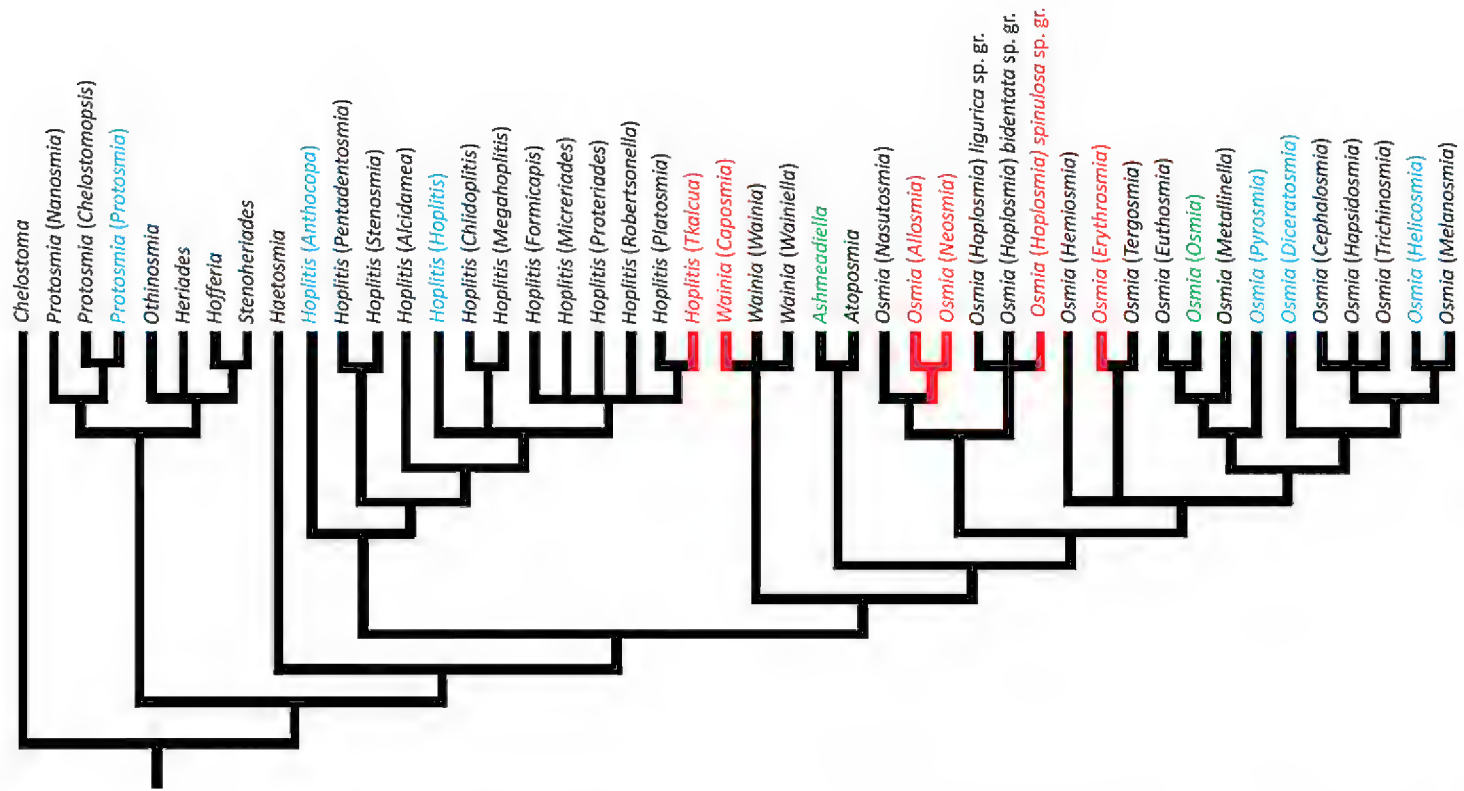


Figure 13. Phylogenetic distribution of snail shell nesting in osmiine bees. Red = taxa that probably exclusively consist of obligate snail shell nesters; blue = taxa that contain both obligate and facultative snail shell nesters (in *Hoplitis* (*Anthocopa*), only one (exclusive) snail shell nester is known); green = taxa that probably contain only facultative snail shell nesters; black = taxa that do not contain any snail shell nesters to the present knowledge (nesting biology of *Hoplitis* (*Megahoplitis*), *Hoplitis* (*Platosmia*), *Wainia* (*Wainia*), *Wainia* (*Wainiella*) and *Osmia* (*Nasutosmia*) still unknown). sp. gr. = species group. Phylogeny based on Praz et al. (2008a), Rightmyer et al. (2013) and Sedivy et al. (2013a).

and fragments of mollusc shells and that transport and bury their shells after nest closure (Tab. 4, Figs 23, 24). In addition, representatives of both subgenera glue patches of leaf pulp onto the shell surface, which is otherwise observed only in one *O.* (*Helicosmia*) species (Fig. 16). These peculiar characteristics common to species of both subgenera suggest close relatedness. In fact, the two subgenera were found to be sister taxa in molecular phylogenetic studies (Praz et al. 2008, Rightmyer et al. 2013). Thus, snail shell nesting in *O.* (*Allosmia*) and *O.* (*Neosmia*) has probably evolved only once in the ancestor of the two subgenera. Given the unsettled phylogenetic relationships among the species groups of *Osmia* (*Hoplosmia*) and the unknown nesting biology of *O.* (*Nasutosmia*) *nasuta* (see Fig. 13), it cannot be excluded that snail shell nesting is the ancestral condition in the *Nasutosmia*-*Allosmia*-*Neosmia*-*Hoplosmia* clade. Under this scenario, the minimal number of independent origins of snail shell nesting in osmiine bees would reduce to eleven.

Two species of *Osmia* (*Allosmia*), probably all species of *O.* (*Neosmia*) and one species of *O.* (*Helicosmia*) glue patches of leaf pulp onto the outer surface of the nest shell before and often also during cell construction and provisioning (Tab. 4, Figs 16, 23). This behaviour has likely evolved twice, probably once in the ancestor of *O.* (*Allosmia*) and *O.* (*Neosmia*) and once in *O.* (*Helicosmia*) *aurulenta*. Its function is still enigmatic. It has alternatively been interpreted as an evolutionary relict inherited from an ancestor that did not colonize preexisting cavities but constructed free standing brood cells



Figures 14–19. **14** Opened nest of *Osmia* (*Helicosmia*) *notata* with brood cells arranged side by side **15** Opened nest of *Osmia* (*Hoplosmia*) *pinguis* with brood cells arranged in a linear series **16** Nest of *Osmia* (*Helicosmia*) *aurulenta* densely covered with patches of leaf pulp **17** Opened nest of *Hoplitis* (*Hoplitis*) *fertoni* with brood cells arranged side by side (photo G. Le Goff) **18** Opened nest of *Osmia* (*Allosmia*) *rufohirta* with single brood cell (photo P. Westrich) **19** Opened nest of *Osmia* (*Neosmia*) *bicolor* with barrier composed of small pebbles and earth crumbs (photo A. Krebs).

(Bellmann 1981), as a camouflage strategy to reduce the optical conspicuousness of the white shells (Grozdanic 1969), or as a means to facilitate the movement of the shell (Malyshev 1937), which, however, is unlikely as several snail shell transporting *O. (Allosmia)* species do not show this behaviour (Tab. 4). Interestingly, instead of gluing patches of leaf pulp on the outer surface of the shell, some *O. (Allosmia)* species, such as *O. melanura* and *O. rutila*, attach portions of leaf pulp to the inner shell surface few millimeters behind the shell opening immediately after selection of a suitable shell for nesting (Müller 1992, Haeseler 1997). Experiments showed that this leaf pulp markings near the nest entrance allow the females to recognize their own nests (Haeseler 1997). Thus, covering the outer shell surface with patches of leaf pulp as observed in other *O. (Allosmia)* species, in *O. (Neosmia)* and in *O. (Helicosmia) aurulenta* might possibly serve the same purpose, i.e. to individually mark the shell and to signal other females that the shell is already occupied.

Species of *Osmia (Allosmia)* invariably construct only one brood cell per snail shell (Tab. 4, Fig. 18). All other obligate snail shell nesters build two or more cells per shell if the available space allows. Most of these species arrange their cells in a linear series (Fig. 15), resulting in the selection of predominantly small to medium-sized shells with narrow whorls. Exceptions among the obligate snail shell nesters are

Table 4. Nest characteristics of osmiine bee species recorded to nest in empty snail shells. For authors of the species names and references see Tab. 3.

Species	Shell surface covered with patches of leaf pulp	Material used for brood cell partitions	Material used for nest plug	Number of brood cells	Arrangement of the cells	Treatment of the sealed shells
<i>Ashmeadiella</i> (<i>Ashmeadiella</i>) spec.	?	?	?	?	?	?
<i>Hoplitis</i> (<i>Anthocopa</i>) <i>conchophila</i>	no	entire brood cells built from petal pieces	?	up to 7	linear	?
<i>Hoplitis</i> (<i>Hoplitis</i>) <i>fertoni</i>	no	mud, sometimes mixed with small pebbles	mud, sometimes mixed with small pebbles	1-8	linear and side by side	not moved
<i>Hoplitis</i> (<i>Hoplitis</i>) <i>pallicornis</i>	?	mud and small pebbles	?	?	?	?
<i>Hoplitis</i> (<i>Tkalcua</i>) <i>zandeni</i>	no	mixture of leaf pulp and sand grains	mixture of leaf pulp and sand grains	1-2	linear	not moved
<i>Hoplitis</i> (<i>Tkalcua</i>) spec. nov.	no	mixture of leaf pulp and sand grains	mixture of leaf pulp and sand grains	1-2	linear	not moved
<i>Osmia</i> (<i>Allosmia</i>) <i>bischoffi</i>	yes	?	?	?	?	?
<i>Osmia</i> (<i>Allosmia</i>) <i>lhotelleriei</i>	no	leaf pulp	fragments of mollusc shells embedded into a matrix of leaf pulp	?	?	transported and buried
<i>Osmia</i> (<i>Allosmia</i>) <i>melanura</i>	no	leaf pulp	fragments of mollusc shells embedded into a matrix of leaf pulp	1	-	transported and buried
<i>Osmia</i> (<i>Allosmia</i>) <i>rufohirta</i>	yes	leaf pulp	layer of small pebbles and earth crumbs followed by a wall of leaf pulp	1	-	transported and hidden (rarely buried)
<i>Osmia</i> (<i>Allosmia</i>) <i>rutila</i>	no	leaf pulp	fragments of mollusc shells, sometimes also small stones embedded into a matrix of leaf pulp	1	-	transported and buried
<i>Osmia</i> (<i>Allosmia</i>) <i>sybarita</i>	no	leaf pulp	fragments of mollusc shells embedded into a matrix of leaf pulp	1	-	transported and buried or hidden
<i>Osmia</i> (<i>Diceratosmia</i>) <i>conjuncta</i>	?	leaf pulp	?	?	?	?
<i>Osmia</i> (<i>Diceratosmia</i>) <i>marilaunidii</i>	?	mixture of leaf pulp and sand	mixture of leaf pulp and sand	?	?	?

Species	Shell surface covered with patches of leaf pulp	Material used for brood cell partitions	Material used for nest plug	Number of brood cells	Arrangement of the cells	Treatment of the sealed shells
<i>Osmia</i> (<i>Diceratosmia</i>) <i>subfasciata</i>	?	mixture of leaf pulp and sand or leaf pulp alone	mixture of leaf pulp and sand or leaf pulp alone	?	?	?
<i>Osmia</i> (<i>Erythrosmia</i>) <i>andrenoides</i>	no	leaf pulp	layer of loosely packed particles (small pebbles, earth crumbs and small plant sticks) followed by two walls of leaf pulp immediately behind each other	1	-	?
<i>Osmia</i> (<i>Helicosmia</i>) <i>aurulenta</i>	yes	leaf pulp	leaf pulp	up to 17	linear and side by side	not moved
<i>Osmia</i> (<i>Helicosmia</i>) <i>chypearis acuta</i>	?	?	leaf pulp	?	?	?
<i>Osmia</i> (<i>Helicosmia</i>) <i>melanogaster</i>	?	leaf pulp	leaf pulp	several	?	?
<i>Osmia</i> (<i>Helicosmia</i>) <i>notata</i>	no	leaf pulp	leaf pulp	up to 18	linear and side by side	not moved
<i>Osmia</i> (<i>Helicosmia</i>) <i>orientalis</i>	?	leaf pulp	-	up to 10	linear	?
<i>Osmia</i> (<i>Hoplosmia</i>) <i>carbo</i>	no	leaf pulp	leaf pulp	1-3	linear	not moved
<i>Osmia</i> (<i>Hoplosmia</i>) <i>croatica</i>	no	leaf pulp	leaf pulp	1	-	?
<i>Osmia</i> (<i>Hoplosmia</i>) <i>fallax</i>	?	?	?	1-4	?	?
<i>Osmia</i> (<i>Hoplosmia</i>) <i>punguis</i>	no	leaf pulp	leaf pulp	2-4	linear	not moved
<i>Osmia</i> (<i>Hoplosmia</i>) <i>spinigera</i>	no	leaf pulp	leaf pulp	?	?	?
<i>Osmia</i> (<i>Hoplosmia</i>) <i>spinulosa</i>	no	leaf pulp	leaf pulp	1-3	linear	turned in situ
<i>Osmia</i> (<i>Neosmia</i>) <i>bicolor</i>	yes	leaf pulp	layer of densely packed particles (small pebbles, earth crumbs, broken mollusc shells, pieces of chalk and wood) followed by a wall of leaf pulp	1-5	linear	turned in situ, partly buried and covered

Species	Shell surface covered with patches of leaf pulp	Material used for brood cell partitions	Material used for nest plug	Number of brood cells	Arrangement of the cells	Treatment of the sealed shells
<i>Osmia</i> (<i>Neosmia</i>) <i>cinnabarina</i>	yes	leaf pulp	layer of densely packed particles (small pebbles, fragments of mollusc shells, petals and stems) followed by a wall of leaf pulp with embedded fragments of mollusc shells and small pebbles	1-3	linear	?
<i>Osmia</i> (<i>Neosmia</i>) <i>jason</i>	yes	leaf pulp	four compartments each limited by walls made of leaf pulp; these compartments are either empty or filled with sand, earth crumbs and small pebbles	2	linear	buried and covered
<i>Osmia</i> (<i>Neosmia</i>) <i>rufigastrea</i>	yes	leaf pulp	layer of densely packed particles (sand grains, earth crumbs, fragments of mollusc shells, stems and blades), followed by a wall of leaf pulp with embedded fragments of mollusc shells	1 to several	linear	transported and buried
<i>Osmia</i> (<i>Neosmia</i>) <i>scutispina</i>	yes	leaf pulp	layer of loosely packed particles (small pebbles, earth crumbs, leaflets or seeds) followed by a wall of leaf pulp	6	linear	?
<i>Osmia</i> (<i>Neosmia</i>) <i>tingitana</i>	yes	leaf pulp	layer of densely packed particles (sand grains, small pebbles, earth crumbs, fragments of mollusc shells and plants) followed by a wall of leaf pulp with embedded fragments of mollusc shells	1-7	linear	turned in situ and covered
<i>Osmia</i> (<i>Osmia</i>) <i>bicornis</i>	?	mud	mud	several	?	?
<i>Osmia</i> (<i>Osmia</i>) <i>cornuta</i>	no	mud	mud	several	?	?
<i>Osmia</i> (<i>Osmia</i>) <i>tricornis</i>	no	mud	mud	several	linear and side by side	not moved
<i>Osmia</i> (<i>Pyrosmia</i>) <i>ferruginea</i>	no	leaf pulp	layer of loosely packed particles (small pebbles, earth crumbs, seeds or leaflets) followed by a wall of leaf pulp occasionally with embedded small pebbles or other particles	up to 10	linear	not moved
<i>Osmia</i> (<i>Pyrosmia</i>) <i>gemmea</i>	?	?	?	?	?	?
<i>Osmia</i> (<i>Pyrosmia</i>) <i>lobata</i>	?	leaf pulp	leaf pulp	3	linear	?

Species	Shell surface covered with patches of leaf pulp	Material used for brood cell partitions	Material used for nest plug	Number of brood cells	Arrangement of the cells	Treatment of the sealed shells
<i>Osmia</i> (<i>Pyrosmia</i>) <i>versicolor</i>	no	leaf pulp	layer of densely packed particles (small pebbles, earth crumbs, pieces of dry blades) followed by a wall of leaf pulp	up to 7	linear	?
<i>Osmia</i> (<i>Pyrosmia</i>) <i>viridana</i>	no	leaf pulp mixed with small pebbles	layer of loosely packed particles (small pebbles, earth crumbs, pieces of dry blades) followed by a wall of leaf pulp mixed with small pebbles	several	linear	?
<i>Protosmia</i> (<i>Protosmia</i>) <i>exenterata</i>	?	resin	resin	up to 5	?	?
<i>Protosmia</i> (<i>Protosmia</i>) <i>glutinosa</i>	?	resin	?	1	?	?
<i>Protosmia</i> (<i>Protosmia</i>) <i>paradoxa</i>	?	resin	resin	?	?	?
<i>Protosmia</i> (<i>Protosmia</i>) <i>sideritis</i>	?	?	?	?	?	?
<i>Protosmia</i> (<i>Protosmia</i>) <i>stelidoides</i>	?	resin	resin	2-4	?	?
<i>Protosmia</i> (<i>Protosmia</i>) <i>tauricola</i>	?	?	?	?	?	?
<i>Wainia</i> (<i>Caposmia</i>) <i>atrorufa</i>	?	large pieces of petals	succession of several partitions of large petal pieces followed by a wall built from a mixture of cemented sand and plant matter	several	linear	?
<i>Wainia</i> (<i>Caposmia</i>) <i>braunsi</i>	?	?	?	?	?	?
<i>Wainia</i> (<i>Caposmia</i>) <i>elizabethae</i>	?	sand grains cemented together with a resinuous substance (saliva?)	layer of loose sand followed by a wall of sand grains cemented together with a resinuous substance (saliva?)	1-3	linear	?
<i>Wainia</i> (<i>Caposmia</i>) <i>gessorum</i>	?	large pieces of petals	succession of several partitions of large petal pieces followed by a wall built from a mixture of cemented sand and plant matter	several	linear	?
<i>Wainia</i> (<i>Caposmia</i>) <i>sexsignata</i>	no	large pieces of petals	succession of several partitions of large petal pieces followed by a wall of leaf pulp	3	linear	?



Figures 20–25. **20** *Osmia* (*Pyrosmia*) *viridana* at nest entrance (photo N. Vereecken) **21** *Protosmia* (*Protosmia*) *paradoxa* on snail shell (photo N. Vereecken) **22** *Osmia* (*Hoplosmia*) *spinulosa* turning its nest in situ **23** *Osmia* (*Allosmia*) *rufohirta* rolling its nest towards a protected place **24** *Osmia* (*Allosmia*) *sybarita* rolling its nest into a self excavated hole in sandy soil (photo N. Vereecken) **25** *Osmia* (*Neosmia*) *bicolor* covering its nest with plant stalks (photo A. Krebs).

H. (Hoplitis) fertoni and *O. (Helicosmia) aurulenta*, which usually colonize medium-sized to large shells and build their brood cells side by side rather than in a linear series, at least in the wide outer shell whorls (Fig. 17).

Several Palaearctic and Afrotropical species of the subgenera *Osmia* (*Allosmia*), *O. (Erythrosmia)*, *O. (Neosmia)*, *O. (Pyrosmia)* and *Wainia* (*Caposmia*) construct a barrier between the outermost cell partition and the nest closure, which most probably contributes to impede the invasion of the nests by predators and parasites (Fig. 19). Depending on the species, this barrier consists of small and often densely packed particles (small pebbles, earth crumbs, plant particles etc.), sand or a succession of parti-

tions (Tab. 4). The construction of such barriers, however, is not restricted to snail shell nesting species but has also been recorded from many osmiine bees nesting in insect burrows in dead wood or in plant stems, particularly of the subgenera *Hoplitis* (*Alcidamea*) and *Osmia* (*Pyrosmia*) (Müller 2018a and references therein).

One of the most fascinating aspects of the biology of snail shell nesting osmiine bees is the way the females treat their nests after having sealed them (Tab. 4, Figs 22–25). While numerous species leave the closed shell without changing its position or orientation, some Palearctic species belonging to three subgenera exhibit specialized behaviours: i) *O.* (*Hoplosmia*) *spinulosa* turns the shell in situ into a particular position with the shell aperture being directed tightly towards the ground (Müller 1994; Fig. 22); ii) *O.* (*Allosmia*) *rufohirta* rolls the shell often over a considerable distance to hide it under vegetation or stones (Bellmann 1981; Fig. 23); iii) several species of *O.* (*Allosmia*) and *O.* (*Neosmia*) transport the shell to a suitable place where it is buried few centimeters deep into the sandy ground (Ferton 1890, Müller 1992, Haeseler 1997, Vereecken and Le Goff 2012; Fig. 24) and iv) two species of *O.* (*Neosmia*) either turn the shell in situ until the aperture is directed towards the ground or bury it shallowly into the ground, before it is completely covered with a dense pile of coniferous needles, grass blades or the like (Grozdanic 1971, Bellmann 1981; Fig. 25). Interestingly, *O.* (*Allosmia*) *sybarita* usually buries the shell into sandy ground (Vereecken and Le Goff 2012), but hides it under low vegetation if the ground is too hard to dig (G. Le Goff personal communication). A similar intraspecific flexibility is observed in *O.* (*Allosmia*) *rufohirta* and *O.* (*Neosmia*) *bicolor*, which occasionally bury the shell at least partly in the ground (Bonelli 1972, Bellmann 1981). These specialized behaviours of turning, hiding, burying or covering of the sealed shells are certainly linked to the protection of the progeny. However, whether they have specifically evolved as a protection against heavy rain, overheating, optically oriented predators or brood parasites remains unclear and needs experimental testing.

Acknowledgments

V. Mauss (Staatliches Museum für Naturkunde Stuttgart) and R. Prosi (Crailsheim) participated in an excursion to southern Morocco, where the nests of *Wainia sexsignata* were discovered. A. W. Ebmer (Puchenau), S. Gess (Albany Museum and Rhodes University Grahamstown), G. Le Goff (Barentin) and J. Ortiz-Sanchez (Universidad de Almería) provided unpublished observations on the biology of snail shell nesting osmiine bees. E. Neubert (Naturhistorisches Museum Bern) identified the snail shells. M.A. Bologna (University Roma Tre) identified the blister beetle pupa and provided literature on *Sitarobrachys*. F. Gusenleitner and M. Schwarz (Biologiezentrum Linz) allowed removal of pollen from collected specimens of *Wainia eremoplana*. G. Le Goff, A. Krebs (Winterthur), V. Mauss, G. Pisanty (Canadian National Collection of Insects, Ottawa), N. Vereecken (Université Libre de Bruxelles) and P. Westrich (Kusterdingen) provided photos. Comments by Jack Neff and Michael Ohl improved the manuscript.

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